

ESTIMATING GRIZZLY BEAR POPULATION SIZE USING CAMERA SIGHTINGS

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Estimating population size of grizzly bears (*Ursus arctos horribilis*) is hampered by certain characteristics (Harris 1986, Interagency Grizzly Bear Comm. [IGBC] 1987, Miller et al. 1987, Miller 1990a): grizzly bears are secretive, aggressive, and difficult to observe; populations often inhabit mountainous, densely vegetated, remote habitats; individual bears often have different probabilities of capture or observation that violate the assumption of equal catchability; age and gender are difficult to determine without handling; sampling opportunities are limited because bears spend 6-7 months in dens; and sample sizes are typically small. These factors impose logistical and financial constraints on researchers obtaining point estimates and confidence intervals (CI's) for the population. The most reliable estimator for grizzly bears is the Petersen capture-recapture design (Miller et al. 1987); it accommodates small samples and requires only a single sighting period after the initial marking period (Seber 1982). The few published estimates of grizzly bear populations have wide CI's (Harris 1986, IGBC 1987, Miller et al. 1987). Model biases are more serious than small-sample bias

because important assumptions are violated (White et al. 1982).

Most advances in estimating population size for grizzly bears have been made using aerial surveys in areas where bears are highly visible (Miller et al. 1987, Miller 1990b). Bears are captured and marked, and subsequently both marked and unmarked bears are "recaptured" or sighted from aircraft in a series of independent searches. This design can produce several types of Petersen estimators that better meet model assumptions and produce larger sample sizes than do standard recapture methods (Minta and Mangel 1989, White and Garrott 1990, Arnason et al. 1991).

In forested habitats where bears are difficult to observe, density estimates are typically converted from combinations of capture data and either telemetry data (DeMaster et al. 1980, Miller and Ballard 1982, McLellan 1989) or observation data (Troyer and Hensel 1964, Martinka 1974, Dean 1976). These methods frequently violate assumptions and usually have no estimate of precision (Harris 1986). The Petersen method has been largely unsuccessful with bears because animals initially are captured using bait and then recaptured using the same technique. For grizzly bears, this procedure violates the model assumption of equal catchability (Seber 1982). In addition, trapping sessions are costly, yet rarely produce adequate

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sample sizes or reliable data (Harris 1986, IGBC 1987, Miller et al. 1987).

We evaluated a self-activating camera for detecting grizzly bears in habitats with limited opportunity for visual sighting. To assess the camera technique as a sighting tool, we describe and evaluate sampling procedures and assumptions, and compare 2 estimators of population size and CI's with the goal of identifying model biases. Our camera technique is compared with other methods used in forested habitats.

STUDY AREA

The study area, in the Swan Mountain Range in western Montana, extended from Highway 2 on the north to the Bob Marshall Wilderness boundary on the south (Fig. 1). This 817-km² area under multiple-use management was chosen for its accessibility and likely geographic barriers on 3 of 4 sides. Grizzly bear movement was restricted on the west and north by the Flathead Valley, with its large, dispersed human population, and on the east by Hungry Horse Reservoir. Grizzly bears could move in and out of the Bob Marshall Wilderness to the south.

The study area was characterized by heavily forested, rugged mountain topography; elevations varied from 914–2,736 m. Over 50% of the area was closed-canopy coniferous forest with the remainder broadly classified as rock lands, avalanche chutes, shrub lands, and timber harvest units.

Using preliminary results on the distribution of marked bears, we delineated a 516-km² core area where radiocollared grizzly bears spent more time and a 301-km² peripheral area (Fig. 1). We emphasized population sampling in the core area and sampled the peripheral area less to assess geographic closure.

METHODS

Initial Capture Method: Snaring

Grizzly bears were opportunistically captured during May and June of 1988–1990. We superimposed a 3.2-km capture grid over the core area and portions of the peripheral area to identify accessible snare sites. Potential sites above snow-line were eliminated, and all sites were within 70 m of the nearest road.

We designed initial capture sessions to mark as many bears as possible within and surrounding the core area by modifying snaring methods and placement (White et al. 1982). Two Aldrich foot snares (Aldrich Animal Trap Co., Clallam Bay, WA 98326) were placed at each site and examined daily for 30–35 days. About 23 kg of wild ungulate bait was maintained at all sites,

and sites were baited for 3–5 days before snares were set. Although the same 61 snare sites were used in 1988 and 1989, snare placement was changed. We used different combinations of wooden cubbies (Jonkel and Cowan 1971) and trail sets each year. In 1990 we stopped snaring in the peripheral area because of lack of captures and sampled 37 sites in the core area. Several short-term snaring sessions were conducted at other times to recapture bears that lost radiocollars.

We marked each bear with an ear tag and a 16.5 × 5-cm Armortite (Cooley Inc., Pawtucket, RI 02862) ear streamer with a unique symbol in each ear. Ear streamers were color-coded for gender. A premolar tooth was extracted for age determination (Stoneberg and Jonkel 1966), and individuals ≥5 years old were classified as adults. Grizzly bears ≥2 years old were fitted with radiocollars. We defined capture rate as the number of snare-nights/capture.

Sighting Method: Cameras

The camera system consisted of a 35-mm fully automatic camera with flash, a passive infrared sensor that differentiated between animal heat and background field, and a 12-volt battery. Bears were photographed approximately every 3 seconds while within the field, and the date of exposure was automatically recorded on each photograph. We placed cameras systematically in the core and peripheral areas in 1989 and 1990 using two 1.6-km grids that were alternated among sessions. Each grid was superimposed on a map of the study area and every third grid cell was selected for sampling. Cameras were placed as central to the grid cell as possible. We used 27–42 cameras/session in the core area.

We conducted 3 camera sessions annually in 1989 and 1990 (Table 1). Cameras were used during the same 3 periods each year to coincide with seasonal changes in food selection (Mace and Jonkel 1986): Session 1 in late spring when grizzly bears consumed herbaceous vegetation, Session 2 in summer when bears ate globe huckleberries (*Vaccinium globulare*) and serviceberries (*Amelanchier alnifolia*), and Session 3 in autumn when bears ate herbaceous vegetation, roots, and large ungulates.

Equal masses of raw meat (wild ungulate or domestic livestock) and 4 L of livestock blood were placed as bait at each camera station. We used about 40 kg bait/station during the first 2 sessions and about 15 kg bait/station thereafter. Supplementary lures varied among sessions and included canned blueberries, anise or vanilla extract, and commercial skunk scent. Each station was arranged around 3 trees. The bait and lure were suspended on a steel cable between 2 trees about 6 m above the ground to disperse scent without providing a reward to bears. We secured the camera 3–3.5 m up a third tree and aimed it at the ground below the bait. To minimize human scent, stations were examined only 2–3 times during a session, and baits were removed at the end of each session.

We defined sampling effort/session (camera-nights) as the sum of all nights that cameras functioned. Sessions did not begin until all cameras were deployed.

Population and Density Estimation

Methods

We defined the sampling unit as a bear independent of its mother (≥ 2 yrs old, except 1 orphaned yearling). To be counted as a sighting, photographs of the same individual at the same camera station had to be separated by an interval of > 24 hours; however, the same bear could be photographed at ≥ 2 stations and be counted as separate sightings within the same 24-hour period. We defined the sighting rate as the number of camera-nights/sighting. Photographs of marked grizzly bears were scrutinized to determine the number of sightings/individual for each session. We also determined which photographs of unmarked bears constituted valid sightings. Within each session, we often were able to distinguish individual unmarked bears by date and location. When several photographs of unmarked bears occurred at the same station on the same day, we used body size, color, and unique markings to differentiate individuals.

We calculated population size for each of the 6 sessions using 2 estimators of the Petersen 2-sample model (Seber 1982:59). During each session, n_1 marked bears were in the core area. A second sample of n_2 bears was sighted by camera, m_2 of which were marked. We first used Bailey's binomial model (Seber 1982:61) employing a bias correction factor to compensate for small sample size (Eberhardt 1990: eq 13). Estimates from this model use aggregated sightings and assume sightings are binomially distributed. The 95% confidence intervals (CI's) for this estimator (\hat{N}_b) were derived from the exact binomial values of the 95% CI of the sighting probability ($\hat{p} = m_2/n_2$) (Overton 1969, Seber 1982). The coefficient of variation (CV) of \hat{N}_b was approximated by $1/m_2^{-0.5}$ (Seber 1982:60-61). We calculated a second population estimate using the Monte Carlo simulation method (Minta and Mangel 1989), which simulates the sighting distribution of unmarked animals from the exact sighting frequencies of marked animals. Using 10,000 simulations/session, we derived a probability distribution and computed a maximum likelihood estimate (\hat{N}_s) and a 95% likelihood interval (abbreviated CI for consistency).

Testing Assumptions of the Petersen Model

The first assumption of the Petersen model is that the target population is geographically and demographically closed during sessions. Because marking was not done during a session, we could not statistically test for closure (Otis et al. 1978, White et al. 1982). Therefore, we used telemetry and cameras to assess closure during sessions using location and survival data

obtained from marked grizzly bears. We located marked grizzly bears ≥ 3 times during each session; those individuals located in the core area ≥ 2 times and known to be alive throughout a session were considered the marked (n_1) sample.

We also assessed geographic closure during the entire 2-year study by constructing a composite home range and comparing capture and sighting rates obtained in the core and peripheral areas. We pooled the location data from 1989 and 1990 to construct 70% and 90% convex polygons (Ackerman et al. 1989). We used 770 aerial locations from individuals composing the n_1 sample during any of the 6 sessions. Polygons were constructed using 1 location/bear/week from den emergence to den entry.

When using the Petersen model, we assumed that marked bears did not lose their marks between the 2 sample periods and that all marks were reported in the second sample. We used visual observation during telemetry flights and photographs to assess loss of marks.

We hypothesized that individual bears were not equally susceptible to baited camera stations. To evaluate sighting heterogeneity, we compared the distribution of empirical sightings with expected sightings derived from the parameters of the empirical distribution (Minta and Mangel 1989). Thus, expected sightings were generated by the binomial distribution function with $n = m_2$, $p = n_1^{-1}$, and $q = 1 - n_1^{-1}$. For each session, we also calculated the variance of the observed sightings (σ^2) and the expected binomial variance, $\sigma_b^2 = npq = m_2 n_1^{-1} (1 - n_1^{-1})$. Sample size permitting, we calculated a chi-square goodness-of-fit test for paired distributions. Cells with expected frequency classes < 1 were grouped. Because of low frequencies, goodness-of-fit results and inferences should be interpreted as indicating trend only (Minta and Mangel 1989).

We compared density estimates (bears/100 km²) of independent marked grizzly bears in the core area during each session to those derived from the binomial and simulation methods. We did not use the boundary strip method (Otis et al. 1978) because densities reflected only marked bears present in the core area each session.

RESULTS

Demography of Marked Grizzly Bears During Sessions

Twenty-seven grizzly bears were captured 52 times in the study area between 1988 and 1990. Three additional bears were captured in the core area at other times. We captured male and female grizzly bears of all age and gender classes except adult females with young. Adult females and their 2-year-olds were captured

only after breakup of family groups. The number and demography of marked grizzly bears differed among sessions and between years because of mortality, egress, and additional captures in 1990. Between 12 and 17 marked bears were in the core area each session (Table 1).

Assessment of Demographic and Geographic Closure

Several individuals living along the edge of the core area could readily enter or exit the photo-grid. However, daily movements of grizzly bears during the 6 sessions averaged 1,569 m (SE = 197 m) (R. D. Mace, unpubl. data), suggesting that individuals moving outside the grid could reenter within 24 hours. There were no birth pulses during the sessions because grizzly bears gave birth during winter. No marked grizzly bears died within the core area during any session, and no human-caused mortalities of unmarked bears were recorded. For this study, we considered the core area closed during the 9–18 days each session was conducted.

Geographic closure of the core area was further demonstrated by comparing snaring and sighting rates with the peripheral area. Twenty-six grizzly bears were captured 51 times in

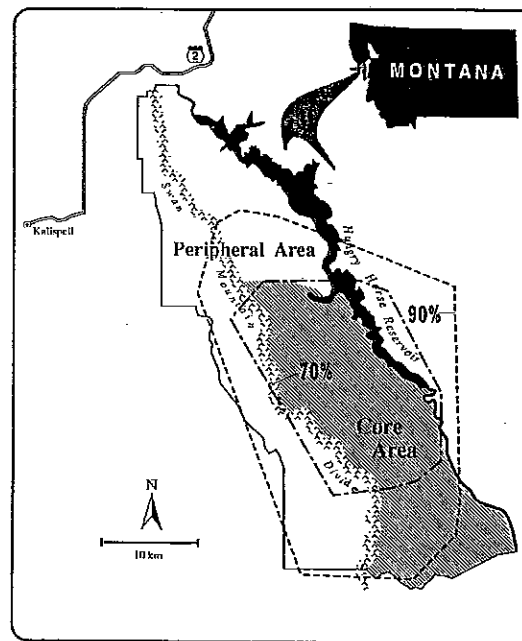


Fig. 1. Convex polygons (70 and 90%) constructed from 770 aerial telemetry locations obtained from 21 grizzly bears showing their relationship to the core and peripheral areas, Swan Mountain Range, Montana, 1989–1990 (data pooled).

3,711 snare-nights in the core area (1 capture/72.8 snare-nights). Conversely, only 1 grizzly bear was snared in the peripheral area in 1,563 snare-nights. We obtained 66 sightings in the

Table 1. Sampling periods, sampling effort, population demography, and sighting rates of marked grizzly bears during 6 photographic sighting sessions in the Swan Mountain Range, Montana, 1989–1990

Characteristics	1989 Sessions			1990 Sessions		
	1	2	3	1	2	3
Sampling period	9–17 Jul	22 Aug–4 Sep	6–17 Oct	11–22 Jul	17–30 Aug	27 Sep–14 Oct
Camera-nights	201	347	465	397	356	468
Cameras/100 km ²	5.2	5.4	8.1	5.2	5.4	5.2
No. marked bears in core area						
Adult male	3	3	3	4	4	4
Adult female	2	3	3	7	7	7
Subadult male	5	4	4	2	2	2
Subadult female	1	0	0	1	2	2
Family group	3	2	2	2	2	2
Marked bears/100 km ²	2.7	2.3	2.3	3.1	3.2	3.2
Bears sighted ^a	11 (6)	14 (8)	12 (4)	8 (4)	2 (1)	3 (2)
Sighting rate ^b	18.3	24.8	38.8	49.6	178.0	156.0

^a Number of sightings of marked bears (no. individuals contributing to sighting).

^b Camera-nights/marked bear sighting.

Table 2. Sighting rates of marked grizzly bear age and gender classes during photographic sessions in the Swan Mountain Range, Montana, 1989–1990.

Age and gender	Year					
	1989		1990		Pooled	
Adult male	12.6 ^a	4/4 ^b	305.2	2/3	20.7	4/5
Adult female	101.3	2/3	407.0	1/7	139.6	2/7
Subadult female	28.1	4/5	407.0	1/2	45.5	4/5
Subadult male	506.5	1/1	1,221.0	1/2	558.5	2/4
Family group	1,013.0	1/3		0/2	2,234.0	1/4

^a Camera-nights/marked bear sighting.^b Number of marked bears contributing to sighting rate/number of marked bears present in core area.

core area in 2,334 camera-nights for a sighting rate of 1 sighting/35.4 camera-nights. Only 1 unmarked grizzly bear was photographed in the peripheral area in 1,249 camera-nights.

Telemetry information also indicated that the core area was important to marked animals throughout the 2-year study. The 70% and 90% convex polygons showed that the marked population had a strong affinity for the core area during the 2-year period (Fig. 1). Movements from the core area were primarily by males captured on the extreme edge of the area.

Photographic Sighting Rates

We obtained 729 photographs of marked (86%) and unmarked (14%) grizzly bears during the 6 sessions. Sixty-six (9%) photographs met our criteria for a valid sighting. Sighting rates (camera-nights/marked bear sightings) of marked bears varied among sessions from 178 during Session 2, 1990 to 18.3 during Session 1, 1989 (Table 1). Marked adult males were sighted most frequently, and most marked adult males and subadult females were sighted (Table 2).

Estimation of Population Size and Density

Individual marked bears responded differently to camera stations resulting in heterogeneous sightability (Table 3). By comparing the 2 models we identified the heterogeneity and gauged its influence on population estimators.

During Session 1, 1989, the observed sighting distribution was similar to the expected distribution based on random binomial sightings ($\chi^2 = 3.39$, 3 df, $P = 0.34$). However, the variance ratio (observed sighting variance to binomial sighting variance; Table 3) of 1.41 indicated a deviation from random sightability; some bears avoided the stations more than expected whereas others were attracted more than expected. The sighting distribution of Session 2, 1989 showed little deviation from expected values with the exception of 1 bear photographed 5 times. That bear contributed to the inflated variance (1.81) and accounted for 92% of the chi-square value ($\chi^2 = 19.22$, 5 df, $P = 0.002$). However, the small sample makes the test result suspect. Session 3, 1989 was similar to Session 1 except that 2 bears were strongly attracted to the stations, producing the highest variance ratio (3.09) of the study. As an indicator, those 2 bears accounted for 86% of the chi-square value ($\chi^2 = 54.0$, 5 df, $P < 0.001$).

Sighting rates were generally lower for 1990 sessions than for 1989. The lower number of sightings contributed to wider CI's compared with 1989 sessions. The variance ratio of 2.13 for Session 1, 1990 reflected the disproportionate attraction to and avoidance of stations. Two bears explained 84% of the chi-square value ($\chi^2 = 23.1$, 3 df, $P < 0.001$). Although estimates for Sessions 2 and 3, 1990 are displayed for comparison (Fig. 2), sightings were too infrequent for valid population estimates. We conclude that the simulation method produced

Table 3. Marking and sighting data and derived variables used in estimating confidence intervals and degree of sighting heterogeneity for grizzly bears in the Swan Mountain Range, Montana, 1989–1990.

Year Session	Marked core area n_1	Number sightings n_2	Number sightings marked m_2	Sighting prob- ability $\hat{p} = m_2/n_2$	CV of N^a	Observed sighting variance ^b	Binomial sighting variance ^c	Sighting distribution of n_1 bears ^d					
								0	1	2	3	4	5
1989													
1	14	12	11	0.92	0.30	1.03	0.73	8	2	3	1		
								6.2	5.2	2.0	0.5	0.1	0.0
2	12	20	14	0.70	1.07	1.81	1.07	4	5	2			1
								3.5	4.5	2.7	1.0	0.2	0.0
3	12	13	12	0.92	0.92	2.83	0.92	8	1	1		1	1
								4.2	4.6	2.3	0.7	0.1	0.0
1990													
1	16	11	8	0.73	0.47	1.00	0.47	12	2		2		
								9.5	5.1	1.2	0.2	0.0	
2	17	4	2	0.50	0.11	0.22	0.11	16		1			
								15.0	1.9	0.1	0.0		
3	17	6	3	0.50	0.17	0.26	0.17	15	1	1			
								14.1	2.7	0.2	0.0		

^a Approximate coefficient of variation of Bailey's binomial estimator.^b Calculated from sighting distribution of the n_1 marked bears.^c Calculated as $npg = m_2 n_1^{-1} (1 - n_1^{-1})$.^d Number of times marked bears were sighted. For example, during Session 1 of 1989, 8 different marked bears were never sighted (0 category), 2 were sighted once, 3 were sighted twice, and one was sighted 3 times. If those 14 bears had been sighted randomly, their sightings would be binomially partitioned, as shown beneath the observed distribution.

inherently less biased population estimates and CI's compared with the binomial model because it simulates the exact form of the sighting heterogeneity.

The density of marked grizzly bears in the core area during most sessions (Table 1) was comparable to those derived from the simulation method. The minimum densities derived from marked bears during 1989 sessions varied from 2.3–2.7 bears/100 km² (Table 1). Using the simulation results and associated 95% CI, density estimates for the 3 sessions in 1989 were: Session 1 ($2.9 \leq 2.9 \leq 3.9$), Session 2 ($2.7 \leq 3.7 \leq 4.6$), Session 3 ($2.5 \leq 2.5 \leq 3.7$). The same comparison for Session 1 of 1990 showed a minimum known estimate of 3.1–3.2 marked bears/100 km² and simulation results of $3.5 \leq 4.1 \leq 7.0$.

DISCUSSION

We used 4 criteria to judge the utility of cameras for sighting grizzly bears in forested habitats. How severely were model assumptions violated? Were adequate photographic

sample sizes obtained and estimators credible? Was the camera method logistically and financially practical? Was our design an improvement over other methods?

Assessment of Model Assumptions

Natural barriers surrounding the study area helped confine grizzly bear movement during sessions. Snaring, camera, telemetry, and survival data provided compelling evidence of demographic and geographic closure during camera sampling.

For closed population models, we assumed that: all animals have the same probability of being caught in the first sample, initial capture does not affect future catchability, and the second sample is a simple random sample. The Petersen model is robust to departures from these assumptions when a systematic rather than a random second sample is taken and by assuming the catchabilities in the 2 samples are independent (Seber 1982, Minta and Mangel 1989, Arnason et al. 1991). Our use of sys-

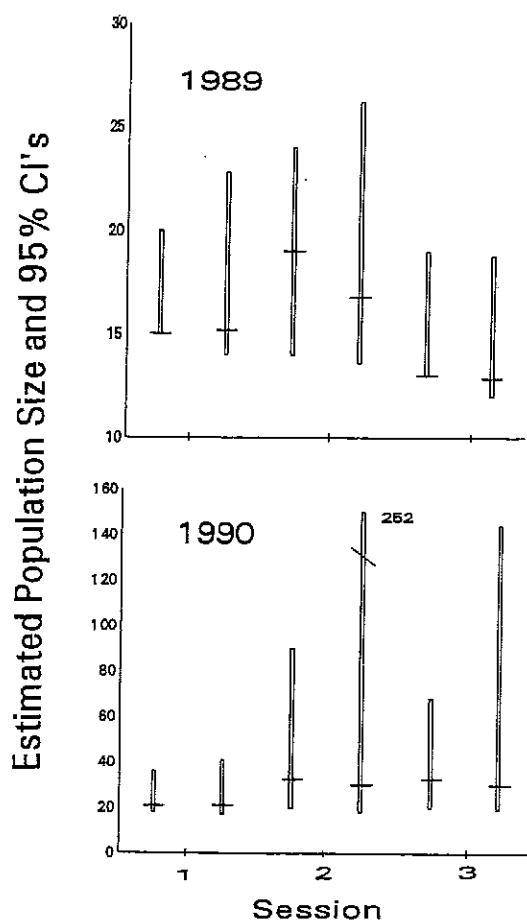


Fig. 2. Population estimate (horizontal bars) and 95% confidence intervals (vertical bars) of total independent grizzly bears in the core area using the Monte Carlo simulation (left bar) and Bailey's binomial (right bar) methods for each sighting session of 1989 and 1990, Swan Mountain Range, Montana.

tematically deployed snares and cameras reduced violations of these assumptions.

Our fundamental sampling problem was unequal catchability during capture and sighting sessions. Any population is likely to contain an uncachable portion and an unequal probability of capture for different cohorts in the first capture. In our study, family groups were the least catchable and sightable cohort. However, because the initial captures were conducted for 3 years, members of family groups that were uncachable during 1 year were even-

tually caught as independent animals. Initial snaring may have affected subsequent sightability with cameras; although both relied on baits, the lures and the amount of human scent present differed, and only snares involved physical restraint. To some degree, these subtle variations in design reduced bias from unequal catchability and sightability (Seber 1982:86).

Sighting rates varied among sessions and between years. We believe the attractiveness of baits to grizzly bears correlated with seasonal availability of preferred foods. Marked bears moved less during the globe huckleberry season (Session 2) than other seasons. This berry crop was judged to be poor in 1989 and grizzly bears were photographed easily. Conversely, an especially good huckleberry crop occurred during 1990; bears moved less, and the sighting rate was low. We obtained low sighting rates during Session 3 of both years because some bears were preparing winter dens and freezing temperatures and snow reduced the effectiveness of baits.

By using photographs and visual observation during telemetry flights, we verified that bears did not lose their marks between marking and sighting. The assumption that all marks are reported on sighting in the second sample was subject to error. Although some sightings may have been missed if bears quickly moved beyond the photographic zone before the camera fired, we had no difficulties determining whether an individual was marked, and we identified all individuals by unique ear streamers.

Photographic Sample Sizes and Estimators

Seber (1982:564-565) concluded that the Petersen model seems to be the most useful method, provided assumptions are satisfied and sufficient recaptures in the second sample are obtained. The binomial model uses only the total number of marked and unmarked bear sightings. Conversely, the simulation method uses the sighting frequencies of marked indi-

viduals, thereby accommodating small sample sizes and sighting heterogeneity. Sighting probabilities were high (0.50–0.92), and the estimates derived from the simulation method were based on adequate sample sizes and produced credible estimates.

Comparisons with Other Approaches

We did not compare the camera method with other sighting methods and we did not know the actual bear density. We know of no method to derive an estimator of precision for population estimates based on capture intensity or telemetry. In forested habitats, few grizzly bear studies have reported point estimates with associated measures of statistical confidence (Harris 1986, IGBC 1987). More commonly reported are density estimates without error terms, derived from the number of known grizzly bears in a given area (Martinka 1974, McLellan 1989). We know of only 1 capture-recapture study using physical recaptures (Hornocker 1962), and the small study area, small sample sizes, and selective capture methods were likely problematic (IGBC 1987). Using observation data from 6 garbage dumps in Yellowstone National Park, Craighead *et al.* (1973) reported that estimates derived from both Petersen and Schnabel methods were comparable to their estimate from direct counts. Unfortunately, computations or results were not documented, details were lacking, and assumptions were ignored (Harris 1986, IGBC 1987). Open population models require large samples and multiple capture periods. We know of none that has been successfully applied to grizzly bears in forested areas. Roop (1980) violated open model requirements that trapping effort be evenly distributed in space and time.

MANAGEMENT RECOMMENDATIONS

Eighty-six percent of 729 photographs were of marked animals. Without this marked sample, we could not have differentiated individuals with enough certainty to meet the as-

sumptions of mark loss and mark reporting. Radiotelemetry also was necessary to evaluate closure. Consequently, there was no evidence suggesting that the technique could be used for grizzly bears without a marked sample.

Because independent methods of initial capture and sighting are desirable, initial capture should use the most effective means for maximizing the marked sample. For grizzly bears in forested habitats, we recommend placing at least 2 snares at each site and varying capture and baiting methods among years. At least 25% of the population (subjective estimate) should be captured, and >50% is preferred. Capture and marking should be done for 3 years to attain a representative sample of adult females and 2-year-olds. We recommend 1 camera session be conducted each year and that stations be placed systematically or randomly each session. The session should be conducted when attractants are not in competition with highly preferred foods. We recommend inverse sampling (Seber 1982:118) where a session is continued until a prescribed number of marked bears are sighted. At some point the assumption of closure would likely be violated and cost may become prohibitive. For our study, annual labor and logistical support cost about \$20,000 and \$14,000/snaring and camera session respectively.

Our camera method offers several advantages over existing sighting techniques. A large study area can be systematically sampled in a relatively brief period, all bears in the population are simultaneously and continuously detectable, and physical capture is unnecessary. These conditions allow better conformance to model assumptions, and are likely to produce larger samples.

Behavioral characteristics of grizzly bears in forested habitats make estimating population size inherently problematic despite improvements in models and field methods. Techniques such as our camera method combined with telemetry may increase sample size and reduce some model biases, but unequal catchability and sightability remain intractable. Use

of different capture methods over several years will reduce intrinsic capture heterogeneity.

A completely independent sighting method would eliminate behavioral "trap" response and relax other model assumptions. This cannot be achieved if attractants are used for both marking and sighting. Detecting grizzly bears either randomly or systematically in forested habitats without attractants is very difficult, although an alternative is to tag bears with radioisotopes and then collect scats (this has not been applied to grizzly bears). Other advances in marking and sighting models (e.g., Arnason et al. 1991) may prove helpful.

SUMMARY

Grizzly bear populations in forested habitats are difficult to estimate, and few studies report point estimates with associated measures of statistical confidence. Experimental designs suffer from logistical problems, model biases, and small sample sizes. We describe a capture-sighting design applicable to forested areas where direct observation of bears is difficult. We reduced bias and increased sample size by using snares for the initial marking period and automatic cameras for the second sample. Capture heterogeneity during the initial marking period was reduced by snaring 27 grizzly bears during 3 years in the same study area in western Montana. Cameras recorded adequate sightings (11–20) in 4 of 6 sessions. Monte Carlo simulation adjusted for severe sighting heterogeneity among marked bears, produced 6 seasonal density estimates and 95% confidence intervals (CI's) ranging from $2.5 \leq 2.5 \leq 3.7$ to $3.5 \leq 4.1 \leq 6.7$ bears/100 km². Sighting rates varied considerably (18–178 camera-nights/sighting), but were generally highest during spring when attractants were more effective. Advantages of our camera method over existing sighting techniques included the ability to sample a large area in a brief period, all individuals are simultaneously detectable, and physical capture is unnecessary. These condi-

tions allowed better conformance to model assumptions.

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LITERATURE CITED

- ACKERMAN, B. B., F. A. LEBAN, E. O. CARTON, AND M. D. SAMUEL. 1989. User's manual for program home range. Second Ed. For., Wildl. and Range Exp. Stn. Tech. Rep. 15, Univ. Idaho, Moscow. 81pp.
- ARNASON, A. N., C. J. SCHWARZ, AND J. M. GERRARD. 1991. Estimating closed population size and number of marked animals from sighting data. *J. Wildl. Manage.* 55:716–730.
- CRAIGHEAD, J. J., J. R. VARNEY, AND F. C. CRAIGHEAD, JR. 1973. Computer analysis of the Yellowstone grizzly bear population. *Mont. Coop. Wildl. Res. Unit, Univ. Montana, Missoula.* 146pp.
- DEAN, F. C. 1976. Aspects of grizzly bear population biology in Mount McKinley National Park. *Int. Conf. Bear Res. Manage.* 3:111–119.
- DEMASTER, D. P., M. C. S. KINGSLEY, AND I. STIRLING. 1980. A multiple mark and recapture estimate applied to polar bears. *Can. J. Zool.* 58:633–638.
- EBERHARDT, L. L. 1990. Using radio-telemetry for mark-recapture studies with edge effects. *J. Appl. Ecol.* 27:259–271.
- HARRIS, R. B. 1986. Grizzly bear population monitoring: current options and considerations. *Mont. For. Conserv. Exp. Stn. Misc. Publ.* 45. Univ. Montana, Missoula. 80pp.
- HORNOCKER, M. G. 1962. Population characteristics and social and reproductive behavior of the grizzly bear in Yellowstone National Park. M.S. Thesis, Univ. Montana, Missoula. 94pp.

- INTERAGENCY GRIZZLY BEAR COMMITTEE. 1987. Grizzly bear compendium. Interagency Grizzly Bear Comm. and Natl. Wildl. Fed., Washington, D.C. 540pp.
- JONKEL, C. J., AND I. M. COWAN. 1971. The black bear in the spruce-fir forest. Wildl. Monogr. 27. 57pp.
- MACE, R. D., AND C. J. JONKEL. 1986. Local food habits of the grizzly bear in Montana. Int. Conf. Bear Res. Manage. 6:105-110.
- MARTINKA, C. J. 1974. Population characteristics of grizzly bears in Glacier National Park, Montana. J. Mammal. 55:21-29.
- McLELLAN, B. N. 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. I. Density and age-sex composition. Can. J. Zool. 67:1,856-1,860.
- MILLER, S. D. 1990a. Population management of bears in North America. Int. Conf. Bear Res. Manage. 8:357-373.
- . 1990b. Detection of differences in brown bear density and population composition caused by hunting. Int. Conf. Bear Res. Manage. 8:393-404.
- , AND W. B. BALLARD. 1982. Density and biomass estimates for an interior Alaskan brown bear, *Ursus arctos*, population. Can. Field Nat. 96:448-454.
- , E. F. BECKER, AND W. B. BALLARD. 1987. Black and brown bear density estimates using modified capture-recapture techniques in Alaska. Int. Conf. Bear Res. Manage. 7:23-35.
- MINTA, S. C., AND M. MANGEL. 1989. A simple population estimate based on simulation for capture-recapture and capture-resight data. Ecol. 70:1,738-1,751.
- OTIS, D. L., K. P. BURNHAM, G. C. WHITE, AND D. R. ANDERSON. 1978. Statistical inference from capture data on closed animal populations. Wildl. Monogr. 62. 135pp.
- OVERTON, W. S. 1969. Estimating the number of animals in wildlife populations. Pages 403-455 in R. H. Giles, ed. Wildlife management techniques. Third ed. The Wildl. Soc., Inc., Washington, D.C.
- ROOP, L. 1980. The Yellowstone grizzly bear: a review of past and present population estimates. Pages 61-75 in R. R. Knight, B. M. Blanchard, K. C. Kendall, and L. E. Oldenburg, eds. Yellowstone grizzly bear investigations. Annu. Rep. Interagency Study Team, 1978 and 1979. Bozeman, Mont.
- SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. Oxford Univ. Press, New York, N.Y. 654pp.
- STONEBERG, R. P., AND C. J. JONKEL. 1966. Age determination in black bears by cementum layers. J. Wildl. Manage. 30:411-414.
- TROYER, W. A., AND R. J. HENSEL. 1964. Structure and distribution of a Kodiak bear population. J. Wildl. Manage. 28:769-772.
- WHITE, G. C., D. R. ANDERSON, K. P. BURNHAM, AND D. L. OTIS. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos Natl. Lab., Los Alamos, N.M. 235pp.
- , AND R. A. GARROTT. 1990. Analysis of radio-tracking data. Academic Press, Inc., New York, N.Y. 383pp.

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